Bothalia: 14, 3 & 4: 587–594 (1983)

Comments on primitive South African crop sorghums and the evolution of sorghum races in Africa

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ABSTRACT

In recent years considerable research has been carried out on cultivated *Sorghum bicolor* (L.) Moench in an attempt to acquire a more complete and meaningful understanding of the taxonomy, classification, origin and evolution of Africa's most valuable cultivated crop. This work has, however, been restricted mainly to the sorghums in northern and central Africa, with southern Africa largely excluded.

In this paper, the morphological variation and distribution of cultivated sorghum races in South Africa is introduced, together with comments on the classification of cultivated sorghums. A new morphological character, the groove at the base of the lower glume of mature, sessile spikelets (developed from a zone of weak, membranous tissue observable in immature spikelets) is evaluated. The degree of development of this groove varies between the different races and is considered to relate directly to their evolution and domestication.

RÉSUMÉ

COMMENTAIRES SUR LES SORGHOS CULTIVÉS D'AFRIQUE DU SUD ET SUR L'ÉVOLUTION DES RACES DE SORGHUM EN AFRIQUE

Durant les récentes années, une recherche considérable a été menée sur le Sorghum bicolor *(L.) Moench en vue de tenter d'acquérir une compréhension plus complète et significative de la texonomie, la classification, l'origine et l'évolution de la culture la plus importante de l'Afrique. Ce travail a cependant été limité principalement aux sorghos du nord et centre de l'Afrique, l'Afrique australe étant en grande partie exclue.*

Dans ce document, la variation morphologique et la répartition des races de sorghos cultivés en Afrique du Sud sont introduites, avec des commentaires sur la classification des sorghums cultivés. Un nouveau caractère morphologique, le sillon à la base de la glume inférieure des épillets sessiles mûrs (développé à partir d'une zone de tissus membraneux faibles pouvant être observée sur les épillets non mûrs) est évalué. Le degré de développement de ce sillon varie entre les différentes races et est considéré comme directement apparenté à leur évolution et domestication.

INTRODUCTION

The last significant input into taxonomic research on South African crop sorghums was made forty-five years ago by Snowden (1936) as part of his world monograph on the group. In more recent years, the importance of sorghum germ plasm and the need for a better and more complete understanding of the morphology, origin, evolution and classification of cultivated sorghums has led to renewed research interest in them. This research, however, has been concentrated around the region of early sorghum domestication of northern and central Africa, to the almost complete exclusion of the crop in southern Africa.

In this paper an attempt is made, at least in part, to update our knowledge of South African sorghum cultivates, and to bring it into line with research undertaken elsewhere in Africa. Morphological and geographical information presented is by no means complete. It is merely offered as an introduction to an extensive survey currently being undertaken on southern African crop sorghums.

In the latter half of the paper the evolution and early migration of cultivated sorghums are discussed. The conclusions presented are based largely, although not exclusively, on a study of southern African material, and are therefore to some extent speculative. To make this work more meaningful and acceptable, there is a need for these conclusions to be more fully tested against material from elsewhere in Africa.

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MORPHOLOGICAL VARIATION

Primitive crop sorghums in South Africa exhibit a wide range in morphological variation. According to De Wet & Huckabay (1966), De Wet & Harlan (1971), De Wet *et al.* (1972) and De Wet (1978), only three races of cultivated sorghum are grown in this region: namely, races Bicolor, Guinea and Caffra. As a result of this investigation, it is now known that all five sorghum races (races Caudatum and Durra included) are cultivated in varying proportions in South Africa. Furthermore, the members of these races hybridize freely and introgress with each other, producing a number of intermediate races.

Race Bicolor (Fig. 1): This race, which most closely resembles the wild sorghums, has a primitive spikelet morphology and is considered to be the least specialized of all the cultivated sorghum races (Harlan & De Wet, 1972; Harland & Stemler, 1976). The inflorescence is characteristically open and paniculate, but may also be subumbellate. The glumes are long (lower: 4,3–5,7 mm; upper: 4,0–5,6 mm) exceeding the grain in length. At maturity they tightly clasp the grain, exposing only its apex. They are mostly smooth and shiny and vary in colour from beige to dark brown, maroon-red and black. The weak membranous zone and basal groove

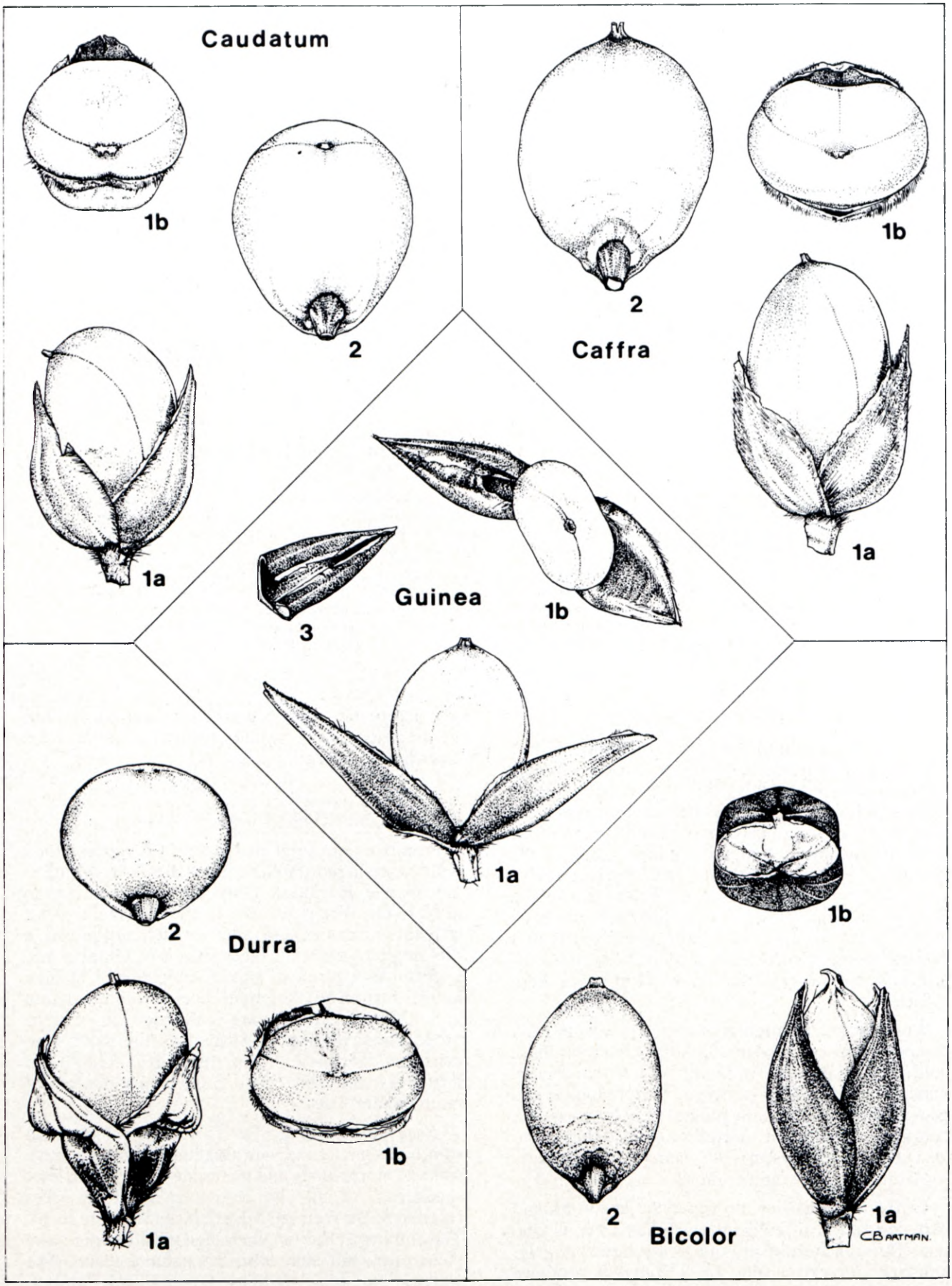

FIG. 1.—Spikelet and grain morphology. 1a & 1b, mature spikelet (a, longitudinal view, b, dorsal view); 2, mature grain (longitudinal view); 3, part of lower glume illustrating turned margins (race Guinea).

(discussed later in this paper) are absent from the lower glume, except where introduced through hybridization and introgression with other races. The grain is relatively small (3,9–4,6 × 2,2–3,1 mm), linear-elliptical in shape and varies in colour from cream to orange-yellow or brown with the exposed apex usually a dark brown or red-brown.

Race Guinea (Fig. 1): Despite its many specialized characters, this race is most closely related to race Bicolor, possessing in common with it the open inflorescence, long glumes and sweet stems. The inflorescence is characteristically open with the branches frequently drooping (pendular). Subumbellate forms have also been recorded. The glumes are long (lower: 4,3–5,0 mm; upper: 4,1–5,2 mm) and exceed the grain in length. At maturity they open and gape, especially the upper glume, the margins of which become strongly inturned. The glumes are generally smooth and shiny, with a limited pubescence, and range in colour from cream-beige to purple, red and black. The zone of weakness and basal groove are present on the lower glume, but are not as broad as in races Caffra and Caudatum. Grain shape is elliptical to discoid (3,3–4,1 × 2,4–3,3 mm). The grains are mostly white coloured with cream and beige-brown grained forms also observed. They are characteristically turned between the glumes, mostly between 55° and 86°. Turning is obstructed in some spikelets due to the grains being tightly clasped by the margins of the lower glumes. Because of the gaping nature of the glumes, the grains are highly exposed and easily dislodged from the spikelet at maturity.

Race Caffra (Fig. 1): In this race the inflorescence may be open or highly compacted, with the majority of individuals having loosely compacted inflorescences which are cylindrical in outline. The glumes are notably shorter than the grain (lower: 3,1–4,4 mm; upper: 3,5–4,5 mm), which they firmly clasp, exposing the upper ½–⅔ of its upper surface. They are smooth and often highly pubescent, giving the spikelet a dull appearance. Glume colour ranges from cream to beige, brown, purple, maroon and black. The zone of weakness and basal groove are highly developed in this race. At maturity the lower glume is distinctly shorter than the upper glume, due to it folding back on itself at the zone of weakness, located at the base of the lower glume. The grains are obovoid to elliptical in shape (3,7–4,8 × 3,0–4,5 mm) with rounded (oval) grains also observed. The colour range is considerable, varying from white to cream, cream-yellow, orange, light and dark brown and red. In the majority of inflorescences examined, between 1–10% of the grains were turned between the glumes, up to a maximum of 58°. This suggests a relatively high incidence of crossing having taken place between races Guinea and Caffra.

Race Caudatum (Fig. 1): Caudatum sorghums closely resemble members of race Caffra, and are considered to have evolved from early members of this race. The inflorescence is loosely or tightly compacted. The glumes, typically black in colour, are shorter in length than the grains (lower: 3,1–4,5 mm; upper: 3,3–4,5 mm), which they firmly clasp, exposing the upper ½–⅔ of the grain surface. The glume surface is smooth and usually pubescent giving the spikelet a dull appearance. The black colour of the glumes contrasts strongly with the predominantly white grains. The zone of weakness and basal groove are well developed as in race Caffra. This race is characterized by an asymmetrical grain, rounded on the inside (back) with the style base displaced out and downwards from the grain apex to a lateral position near the apex of the lower glume, giving the grain a typically 'hunchback' appearance. The grains are obovoid or broadly obovoid in shape (3,7–4,2 × 3,4–4,0 mm). As with race Caffra, many of the inflorescences have grains that rotate between the glumes.

Race Durra (Fig. 1): This race is markedly distinct from other cultivated sorghum races. The inflorescence varies between compact and loosely compact. The glumes are shorter than the grain (lower: ±4,0 mm; upper: 4,0–4,1 mm), exposing the upper half of its surface. Both glumes have a transverse medial crease or fold which characterises this race. Below the fold the glume is hard and cretaceous while the upper half is normally soft and leathery. The cream-orange grains are large (4,1 × 4,3 mm), and obovoid in shape with a broad somewhat flattened apex and triangular base. The basal groove and zone of weakness associated with the lower glume in most other races is absent in this race.

Intermediate races: Intermediate forms between the different races are common, often exhibiting a continuous range in variation between parent races. De Wet (1978) recognizes three intermediate races from South Africa, which are synonomous with four of the cultivated *Sorghum* species recorded from this country by Snowden, namely:

1. Caffra × Bicolor = *S. basutorum*
2. Bicolor × Guinea = *S. millitium*, and *S. roxburghii*
3. Bicolor × Durra = S. *subglabrescens*

An additional four intermediate races have been identified during this study.

4. Caffra × Guinea
5. Caffra × Caudatum
6. Bicolor × Caudatum; and
7. Guinea × Caudatum.

Besides the usual two way crosses, a few plants have been observed which exhibit a combination of characteristics from three races, namely, races Caffra × Caudatum × Bicolor. The typical characters of each race may or may not necessarily be equally well represented in the compound intermediate form.

DISTRIBUTION

No attempt is made by Snowden (1936) to outline the distribution of the eight species of cultivated sorghum recorded by him for South Africa. He merely cites specific localities where these are known. This is understandable due to the limited amount of South African material at his disposal which does not lend itself to accurate geographical extrapolation. The most recent accounts of cultiva-

ted sorghum distributions in South Africa are by De Wet & Huckabay (1966), De Wet & Harlan (1971), and De Wet *et al.* (1972 & 1976), all of whom appear to have based their distributions of cultivated South African sorghums largely on Snowden's (1936) outdated work. It is impossible at this stage of the current investigation of cultivated South African sorghums to give an accurate updated account of their distribution, as only part of the region has been sampled to date and in many cases in insufficient detail. The distributions oulined below are therefore incomplete, but do, nevertheless, give a more realistic account of the situation than is available in existing literature.

Race Caffra: This is grown purely as a grain sorghum, and is the most widespread and abundant race in South Africa. It is known to be cultivated in northern Namibia (South West Africa), northern and eastern Botswana and the entire eastern half of South Africa.

Race Guinea: This race is grown equally for its sweet stems and grain. It is slightly less widespread and less commonly grown than race Caffra. Its distribution extends from the northern and eastern Transvaal, through Swaziland to northern Natal (Zululand).

Race Bicolor: Members of this race are cultivated almost exclusively for their sweet stems. They are generally less commonly grown than the two former races. The distribution includes northern Namibia, the south-western Transvaal (Bophuthatswana), the north-eastern Transvaal (Venda) and north-western Transvaal (Lebowa).

Race Caudatum: This race has not previously been recorded from South Africa. It is not as abundant as races Caffra, Guinea or Bicolor. Its current distribution includes collections from various localities throughout Venda and only one collection from Lebowa. Caudatum sorghums lack the sweet stems of Bicolor and Guinea sorghums and are therefore grown exclusively for their grain.

Race Durra: Previously unrecorded from South Africa except for *S. subglabrescens* (Snowden, 1936) regarded by De Wet (1978) as an intermediate race between races Bicolor and Durra. Only two collections have been made to date, both from a single village in Venda. It is cultivated exclusively for its grain.

CLASSIFICATION

Until recently, Snowden's (1936) classification was used almost exclusively for South African crop sorghums. This classification is far from satisfactory, but with nothing better to take its place, is still in use. Its many shortcomings are outlined by Harlan & De Wet (1972). The most realistic treatment of cultivated sorghums to date is that of De Wet & Huckabay (1966) and De Wet (1978). Their biological species approach is practical and particularly well suited to crop plants, and provides an acceptable solution to the problems encountered in cultivated sorghum classification. This system of classification, which was later extended by Harlan & De Wet (1971) to include all cultivated plants, is not, however, exempt from criticism. In this regard support is given to the comments made by Westphal (1974).

The division of a species, containing both wild and cultivated members, into two subspecies is unacceptable as it clashes directly with the use of subspecies in conventional taxonomy, and disregards geographic separation as a delineating criterion. Remoulding of the subspecies concept, as Harlan & De Wet (1971) have done, to accommodate cultivated plants strongly contradicts their support for Jeffrey (1968) who proposed that formal botanical categories and nomenclature should not be used for cultivated plants at the infraspecific level. It also contradicts their decision not to use variety as a botanical term for cultivated plants, on the grounds that this would cause confusion. The need to distinguish between cultivated and wild taxa within a single species is not totally without support. It is considered undesirable, however, to do this by creating a special category.

No immediate objection can be found for using race and subrace as infraspecific ranks for cultivated plants. The recognition of a fifth taxonomic rank below that of cultivar, namely, line, clone and genome, is contrary to the code which designates cultivar as the lowest category for cultivated plants.

The concept of race as defined by Harlan & De Wet (1971) represents a hybridization of the formal taxonomic categories subspecies and variety, and is considered suitable as the basis for the initial grouping of cultivated plants within a species. Similarly, subrace is seen as an acceptable means by which to identify convenient divisions within each race. The use of race and subrace, by Harlan & De Wet, as subdivisions for infraspecific wild taxa is unjustified. Not only is it contrary to the Code, but also attempts to destroy part of a generally accepted system which has been in use for a considerable period of time. Furthermore, and perhaps even more important, it is not seen as an improvement over the system currently in use. It seems strange that these authors, who support not using formal taxonomic categories for cultivated plants, can at the same time promote the idea that categories created by them for cultivated plants are suitable for use with wild taxa.

NEW SUPPORTING EVIDENCE

This study of cultivated sorghum races in southern Africa has brought to light a new character which supports the conclusions of De Wet & Harlan (1971), De Wet *et al.* (1972 & 1976), Stemler *et al.* (1975), De Wet (1978) and Harlan & Stemler (1976) regarding the evolution and early movement of cultivated sorghum races in Africa.

The character presents itself in two forms depending on the age of the spikelet (Fig. 2). In the immamature, sessile spikelet it exists as a thin membranous zone situated at the base of the lower (outer) glume. In the mature spikelet it is seen as a groove at the base of the glume. Both the

membranous zone and the groove are differentially developed in the different races, being absent in race Bicolor and Durra, well developed in Caffra and Caudatum and intermediate in race Guinea. It should be pointed out that all reference to these characters and the extent to which they are developed in the different races is directed strictly at the typical forms within each race. Because of hybridization and introgression, individuals have been observed in which this character is atypical of the race in which they are naturally placed. In most of these cases, however, the intermediate nature of the plants can be determined.

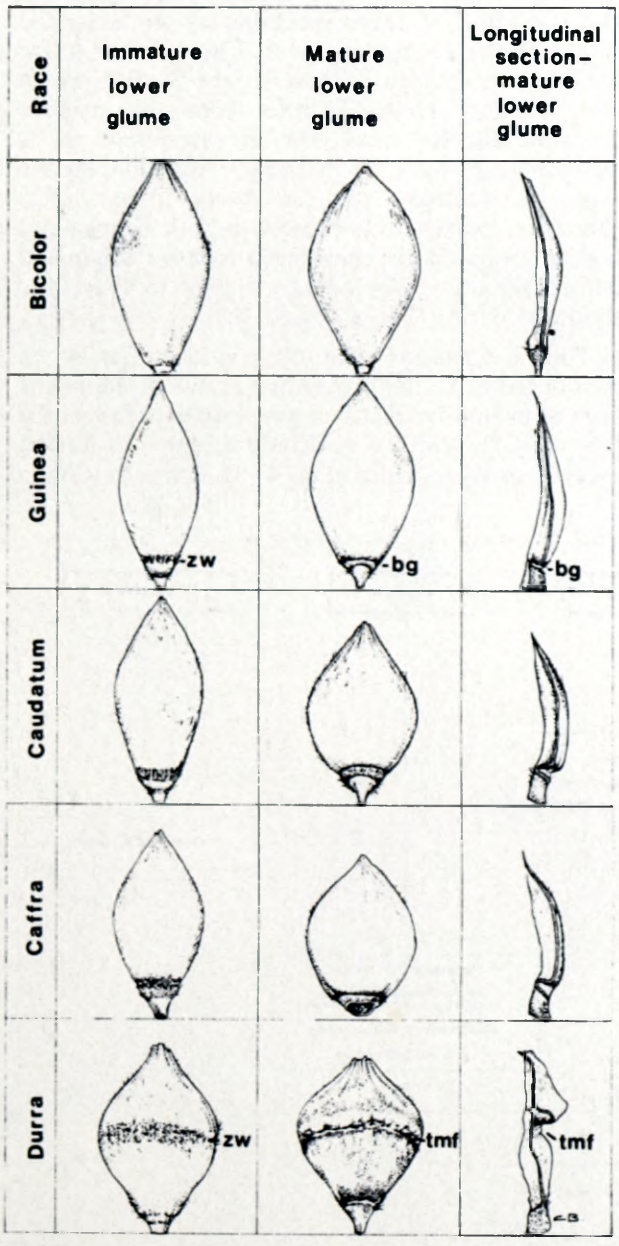

FIG. 2.—Structure of lower glume. zw, zone of weakness; bg, basal groove; tmf, transverse medial fold.

DEVELOPMENT OF THE BASAL GROOVE

The basal groove is located at the base of the lower glume of the mature fertile spikelet. It is not present on the upper glume. It develops from the weak membranous zone of tissue present in immature spikelets. As the grain matures and swells the lower glume, as it is pushed outwards, folds back on itself along the zone of weakness resulting in the formation of the basal groove. The zone of weakness is hidden in the mature spikelet inside the groove and is often further obscured by the long hairs concentrated at the glume base. The effect of the formation of the groove is to shorten the apparent length of the lower glume. This is particularly pronounced in races Caffra and Caudatum (Fig. 2).

SELECTIVE ADVANTAGE OF THE ZONE OF WEAKNESS

The presence and degree of development of the zone of weakness is considered to have arisen as of a direct selective response to domestication, the advantage of which is realized during the threshing of the grains.

In race Bicolor (Fig. 1) the glumes of the fertile spikelet tightly clasp the grain. This condition is disadvantageous during threshing as it prevents easy separation of the grain from the spikelet. Furthermore, it would also result in an increased incidence of shattering of the grains due to prolonged and more intensive stamping needed to dislodge the grain during threshing. Shattered grains are highly undesirable as the small fragments are difficult to separate from the chaff during winnowing. Race Bicolor is cultivated largely for its sweet stems rather than for its grain. In South Africa it is grown almost exclusively for this purpose. Selection favouring threshing is therefore minimal and would account for the zone of weakness being absent in the typical forms of this race.

In races Guinea, Caffra and Caudatum, which are cultivated primarily for their grain, threshing is made easier by the presence of the zone of weakness. During threshing the lower glume breaks away from the spikelet along the weak membranous tissue at its base, enabling the grain to be more readily separated from the spikelet.

The extent to which the zone of weakness is differentiated in these races can also be correlated with threshing. In race Guinea (Fig. 2) the membranous zone although present is not as broad as in race Caffra or race Caudatum. This is considered to be due to Guinea sorghums having evolved in the wetter, more humid environment of West Africa. In this race the inflorescence branching has remained open and specialization has produced fertile spikelets with glumes that open and gape together with discoid grains that turn between the glumes. These are important adaptations enabling the inflorescence and spikelets to dry out more easily in the wet West African climate. This specialization strongly favours easy separation of the grains from the spikelet during threshing, and would, therefore, have negated any further need for the zone of weakness continuing to develop.

The zone of weakness is best developed in races Caffra and Caudatum (Fig. 2). In these races the glumes firmly clasp the lower portion of the grain. A well-developed zone of weakness is therefore desirable in order to facilitate easy grain removal

during threshing. Release of the grain may also be helped by the shortness of the glumes in these two races.

The absence of the zone of weakness at the base of the lower glume in race Durra, adds support to an independent origin of this race from primitive Bicolor sorghums. In Durra sorghums separation of the grain during threshing is helped by the transverse medial folds on each glume (Fig. 2). These folds are equivalent to the basal groove in other races, and develop from zones of thinner, weaker tissue present on both glumes of the fertile spikelet. During threshing the upper halves of the glumes would break away at these zones thus enabling easier release of the grains from the spikelets.

EVOLUTION AND EARLY MOVEMENT

A schematic outline illustrating the lines of evolution and specialization of the five cultivated sorghum races is presented in Fig. 3. The wild progenitors of cultivated sorghums are believed to be members of *S. bicolor* subsp. *arundinaceum*, either from race Aethiopicum or race Verticilliflorum or possibly from a complex involving both these races (De Wet, 1976).

Cultivation of the wild progenitor led to the origin of a primitive Bicolor cultivate (Fig. 3–A), characterized by non-articulating spikelets and enlarged grains (De Wet *et al.*, 1972). Primitive Bicolor sorghums are considered to have given rise to two distinct evolutionary lines. The first line (Fig. 3–B1) includes race Durra, considered by Harlan and Stemler (1976) to have evolved in Asia independently of the other sorghum races, and later reintroduced back into Africa (Fig. 4–2). Race Durra is distinct from other sorghum races, particularly in the size and form of the grains and the transverse medial folds across both glumes of the fertile spikelet. It is considered to be linked somewhat distantly to race Bicolor through primitive Bicolor sorghums. These two races share in common the absence of the zone of weakness and groove at the base of the lower glume.

The second line of evolution from primitive Bicolor (Fig. 3–B2) is responsible for producing the four remaining sorghum races. The most primitive and least specialized of these is race Bicolor, which has probably changed little from the original primitive Bicolor stock. At an early stage in its development, some of its members developed the zone of weakness on the lower glume. This character, because it is present in both Guinea and Caffra sorghums, is considered to have originated before primitive Bicolor was moved to West and southern Africa (Fig. 4–1a & 1b).

This specialized form of primitive Bicolor is considered to be the progenitor of two independent lines of evolution. Firstly it gave rise to race Guinea (Fig. 3–C1), which is generally accepted as having evolved in West Africa (Fig. 4–3). Specialization in

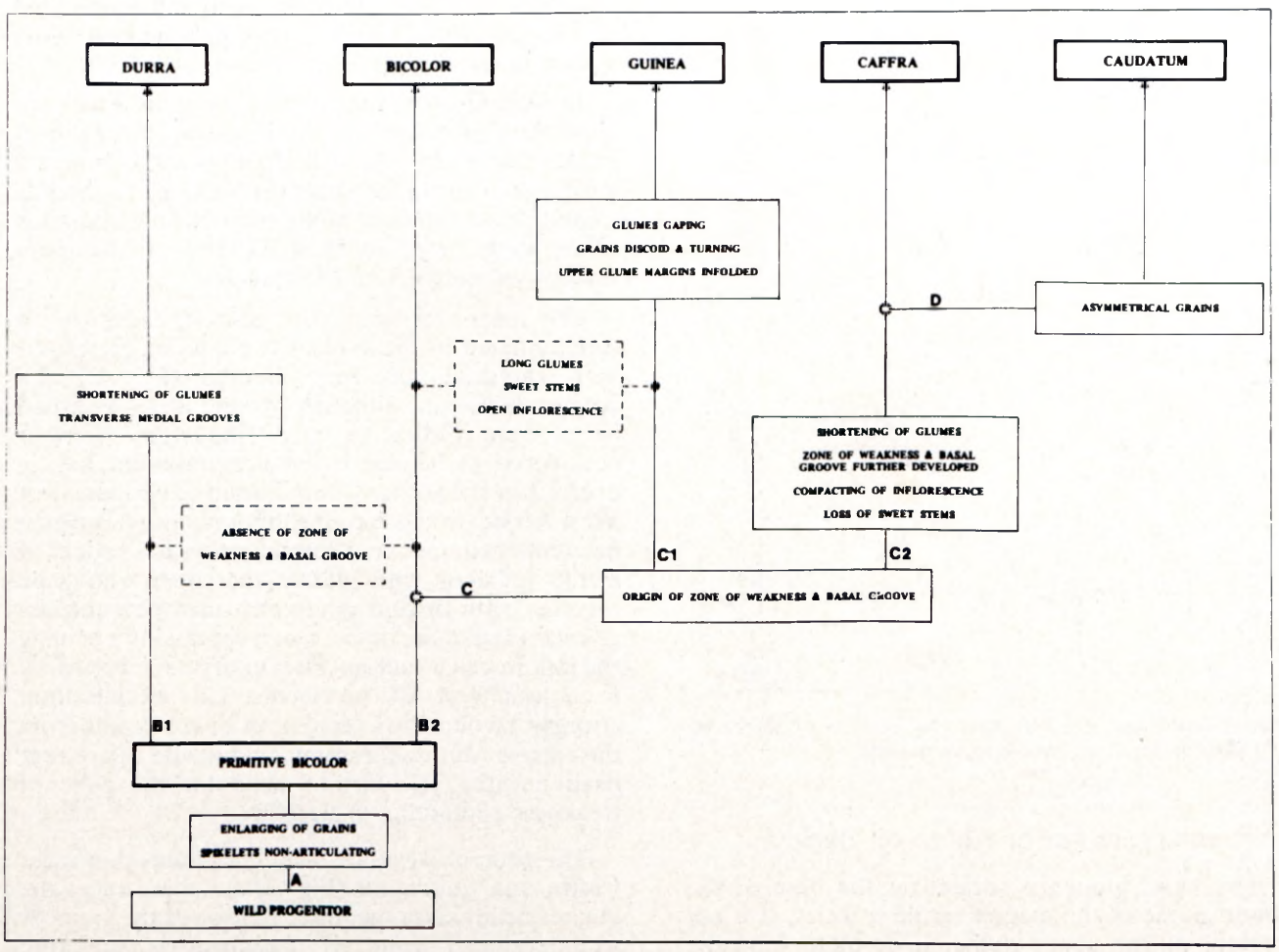

FIG. 3.—Schematic outline illustrating lines of evolution and specialization of the five cultivated sorghum races.

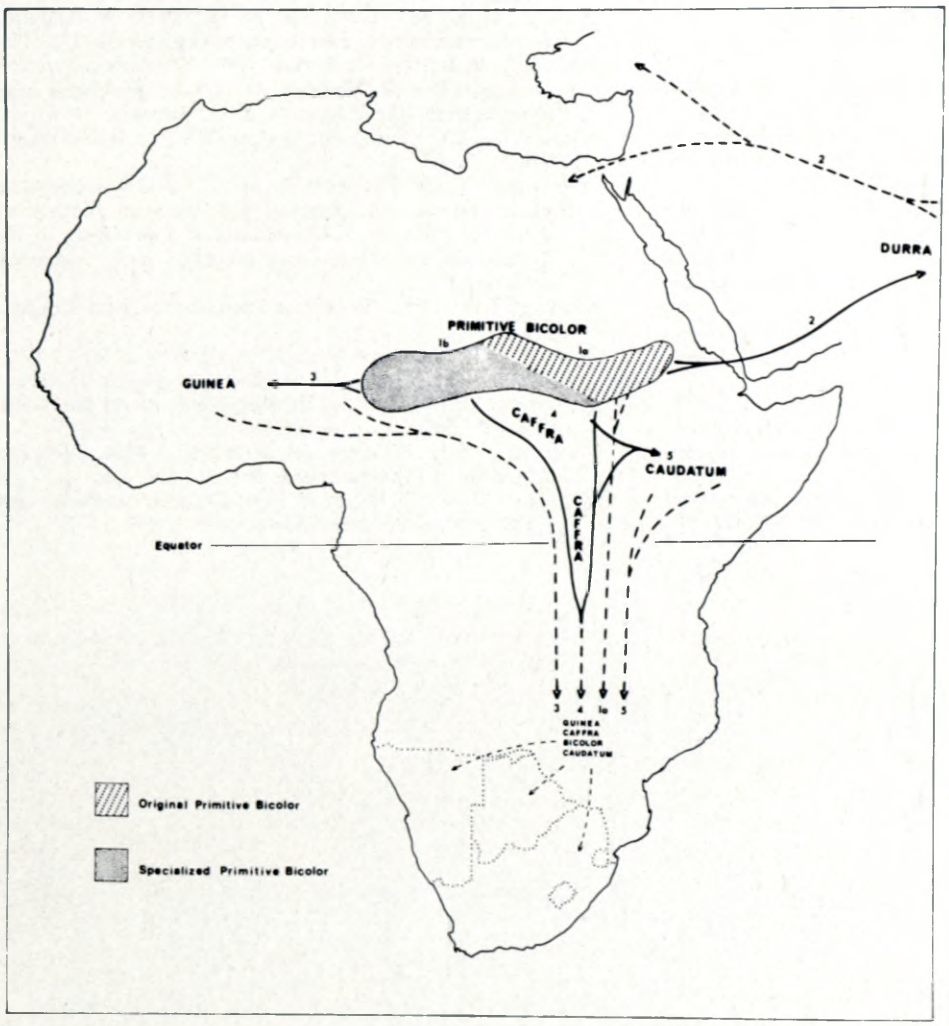

FIG. 4.—Early movement of cultivated sorghum races (adapted from Harlan & Stemler, 1976). ——→ representing movement before or during primary specialization. ---------→ representing movement after primary specialization.

this race reflects an adaptation to a wet environment, and is characterized by the open, gaping glumes and turned discoid grains (Stemler *et al.*, 1975; De Wet *et al.*, 1972), as well as the upper glume having strongly inturned margins. Race Guinea is most closely related to race Bicolor. Characters shared by these two races, but absent in races Caffra, and Caudatum, include long glumes which exceed the grain in length, a primitive open inflorescence and sweet stems. The zone of weakness and basal groove are less developed in this race than in races Caffra and Caudatum.

The second line of evolution from specialized primitive Bicolor is the Caffra line, which includes races Caffra and Caudatum (Fig. 3–C2). Evolution of this line probably started sometime before the migration of cultivated sorghums southwards, with selection favouring the compacting of the inflorescence, further development of the zone of weakness, shortening of the glumes and the loss of sweet stems, due to a preference towards grain production. This specialization probably continued during the early parts of the movement of primitive Caffra southwards (Fig. 4–4), but would have been largely complete by the time the equator had been reached. Race Caffra is, therefore, not seen as having had an independent origin in the southern part of Africa, presumably from race Verticilliflora, as suggested by De Wet & Harlan (1971) and Schechter & De Wet (1972).

Race Caudatum is morphologically very similar to race Caffra, sharing with it all the specialization of the Caffra line of evolution. The distribution of present-day race Caudatum is concentrated in central and eastern Africa which, together with the morphological features shared with race Caffra, suggests that it is a derivative of race Caffra (Fig. 3–D), developed from members of this race remaining behind in central Africa after the movement of race Caffra into southern Africa (Fig. 4–5). Race Caudatum has a single derived character, the asymmetrical grain, not present in typical Caffra sorghums. All available evidence, therefore, points to race Caudatum being of recent origin, as concluded by Harlan & Stemler (1976), rather than being a relatively old race because it occupies an area of first sorghum cultivation, as proposed by De Wet *et al.* (1976).

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